

Higher Body Temperatures and Earlier Parturition in Response to Hypoxia Experienced by Pregnant Lizards

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Abstract Many species are shifting towards higher altitudes in response to global warming, but how these upslope-shifting species will respond to hypoxic environments at high altitudes remains unclear. Hypoxia can be especially challenging for viviparous reproduction because of the limitation of oxygen supply to the female and her developing embryos. To investigate the effect of hypoxia on viviparous females and their offspring we acclimated pregnant females of a high-altitude dwelling viviparous lizard (*Phrynocephalus vlangalii*) to local oxygen and hypoxia conditions, respectively. We then recorded maternal body temperatures, postpartum body condition, as well as offspring morphology and locomotor performance. We found that pregnant females had higher body temperatures and advanced their parturition under hypoxic acclimation. However, maternal body condition, offspring morphology and locomotor performance were unaffected by the hypoxic conditions during gestation. Our study suggests that upslope-shifting viviparous lizards respond to hypoxic environments by plastically adjusting their body temperatures to reduce parturition time, without short-term costs to offspring traits.

Keywords climate change, hypoxia, offspring, pregnant female, reproduction, viviparous lizard

1. Introduction

Species from diverse regions around the world are shifting their distributions towards historically cooler regions in response to global warming (Parmesan and Yohe, 2003; Hickling *et al.*, 2006; Thomas, 2010). Research on terrestrial vertebrates in mountain regions has documented frequent shifts towards higher altitudes in the past decades (Chen *et al.*, 2011; Freeman and Freeman, 2014; Bani *et al.*, 2019), but how these species will respond and potentially adapt to their new hypoxic environments at higher altitudes remains unclear.

Successful reproduction plays an essential role in stabilizing population dynamics and species maintenance (Manlik, 2019). Pregnancy reduce a female's capacity for optimal ventilation and supply of oxygen (Munns and Daniels, 2006; Munns, 2013), creating a mismatch between the increasing oxygen consumption of the developing embryos (DeMarco, 1993). This mismatch makes viviparous reptiles potentially vulnerable to hypoxic environments because of their extended gestation time and minimal placental connection between embryos and the maternal body (Blackburn, 1993). In pregnant females food consumption decreases as parturition approaches because the developing embryos increasingly occupy more space in the abdominal cavity (Munns and Daniels, 2006). Despite this, pregnant females are able to increase (or at least maintain) their metabolism under the burden of large developing embryos (Robert and Thompson, 2000; Munns, 2013). With respect to the developing embryos, a decrease in oxygen supply during gestation may reduce developmental success and result in offspring with less-than-optimal morphological and performance traits (Herman and Ingermann, 1996; Sun *et al.*, 2014). If pregnant females are exposed to severely hypoxic

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conditions during late-term gestation, premature parturition may occur (Timmerman and Chapman, 2003).

Reptiles are known to be plastic in their behavior, physiology, and life-history (Bellard *et al.*, 2012; Huey *et al.*, 2012; Wong and Candolin, 2015), which may help buffer hypoxic stress. For example, pregnant lizards lower their body temperatures during gestation, which potentially reduces both maternal and embryonic oxygen consumption (Mathies and Andrews, 1997). When acclimated to hypoxic conditions, adult lizards select lower body temperatures, which lowers their metabolic costs (Li *et al.*, 2020). Lizards translocated to higher altitudes respond to hypoxic conditions by enhancing the oxygen delivery capacity of their cardiovascular systems (He *et al.*, 2013; Kouyoumdjian *et al.*, 2019). Smaller offspring size has also been documented as a result of oviparous embryos developing under hypoxic incubation conditions (Liang *et al.*, 2015). However, which of these potential strategies may be used by reptiles when exposed to hypoxic environments, and whether they can mitigate negative effects on pregnant females and their offspring remains unclear.

To better understand how viviparous reptiles respond to hypoxic conditions we used a high-altitude-dwelling (~2000–4500 m a.s.l.) viviparous lizard—the Qinghai toad-headed lizard (*Phrynocephalus vlangalii*) distributed across the Qinghai-Tibet plateau (Zhao *et al.*, 1999)—as our study system to address the following questions: (1) how do pregnant females respond (in terms of behavior, physiology, and life-history) to the hypoxic environment? and (2) is the species able to avoid negative impacts on pregnant females and their offspring using strategies to mitigate the effects of hypoxia on reproduction? We acclimated pregnant lizards approaching parturition (from a population at ~3600 m) to their local oxygen conditions (3600 m; “Control” treatment), and to higher altitude oxygen conditions (4600 m; “Hypoxia” treatment) in summer, respectively. This experimental design mimics the scenario of species shifting upslope for 1000 m to compensate for an increase of 6 °C due to global warming (the annual mean air temperature at Qinghai-Tibet plateau is predicted to increase by 6.4 °C [RCP8.5] by the end of the 21st century; Zhao and Wu, 2019). We compared maternal body temperatures during gestation, postpartum body condition, reproductive output, plus offspring body mass, snout-vent length, and sprint speed between lizards from the Control and Hypoxia treatments. Based on results from existing studies on the response of other reptile species to hypoxia (Hicks and Wood, 1985; Herman and Ingermann, 1996; Timmerman and Chapman, 2003; Kouyoumdjian *et al.*, 2019), we propose two hypotheses: (1) pregnant females will select lower body temperatures in response to the Hypoxia treatment; and (2) pregnant females will produce offspring with smaller body size and/or lower

sprint speed in response to the Hypoxia treatment.

2. Materials and Methods

2.1. Study species and Hypoxia treatment In July 2019, we collected 24 late-term pregnant female *Phrynocephalus vlangalii* from a population in Aksay, Gansu Province, China (altitude of ca. 3600 m). All individuals were collected within 2 days. According to a previous study, *P. vlangalii* from similar elevations (ca. 3470 m) have a reproductive season from May to August (Wu *et al.*, 2015). We ensured females were in late-term pregnancy and minimized the variation of reproductive stages among collected individuals by abdominal palpation (Husak, 2006; Zani *et al.*, 2008). We measured the snout-vent length (SVL) and body mass (BM) of each female and randomly assigned them into one of two experimental groups: Control ($n = 12$) vs. Hypoxia treatment ($n = 12$). Within 2 days of capture, female lizards were transported to our laboratory in Beijing, China (altitude of ca. 53 m), where they were immediately placed in their designated acclimation treatments. Within each treatment, pregnant females were randomly housed in two plastic terraria ($47 \times 35 \times 24$ cm³; 6 individuals in each), which were kept in two separate O₂-controlled incubators ($56 \times 43 \times 94$ cm³; Huaxi Electronics, Changsha, China), with fresh air continually flushed through the system. We adjusted the concentration of oxygen to 13.86% and 12.12% in the Control and Hypoxia incubators, respectively, to simulate the oxygen conditions at 3600 m and 4600 m, respectively (equivalent PO₂; the lab was close to sea level). All O₂-controlled incubators were located in a climate-controlled room with a constant air temperature of 16°C. Inside the incubators we used a full-spectrum bulb (35 w, UVA+UVB) to heat one end of each terraria from 8:00 to 20:00 (simulating the summer daylight hours at the field site). This created a thermal gradient (~28–55 °C) allowing the lizards to behaviorally thermoregulate. The laboratory thermal gradient covered the range of active body temperatures measured in the field (~31–36 °C; Jiang Z. W., unpublished data). We put a layer of sanitized sand (2 cm in depth) on the bottom of each terraria. Food (mealworms and crickets dusted with vitamins and minerals) and water were provided *ad libitum*. Every ten days we shifted the position of terraria within each experimental group to minimize any differences in oxygen levels and temperature within the O₂-controlled incubators and the climate-controlled room.

2.2. Maternal body temperatures and reproduction We measured the body temperatures (T_b) of pregnant females twice before parturition (on days 5–6 and 18–19 of the experiment). Cloacal temperatures of each individual were recorded with a calibrated thermometer (UT325; Shenzhen Meter Instruments, Shenzhen, China; 0.1 °C resolution). To minimize interruption

to the lizards' thermoregulatory behavior, we conducted maternal body temperature measurements over 2 days. We measured body temperatures at 9:00, 11:00, 13:00, 15:00, 17:00, 19:00 on the first day, and 10:00, 12:00, 14:00, 16:00, 18:00 on the second day. We restricted the maximum time for measuring body temperature of each individual to 10 seconds and kept the interruption to other females in the same container as minor as possible. Additionally, for each treatment we monitored temperatures at the hot and cool ends of terraria (on the sand surface), every 30 minutes with iButtons (DS1921, MAXIM Integrated Products Ltd., USA, ± 0.1 °C resolution), to quantify the thermal gradient experienced by the lizards. We checked terraria three times a day for parturition. Upon parturition, we recorded the date and measured the snout-vent length (SVL, ± 0.01 mm) and body mass (BM, ± 0.001 g) of the pregnant females and their offspring.

2.3. Locomotor performance of offspring Within 2 days of parturition, we measured sprint speeds of offspring. Hatchling lizards were acclimated at 34 °C (preferred body temperature; Jiang Z. W., unpublished data) for 2 hours before their locomotor trials began. Each lizard was then encouraged to run along a 1-m racetrack with 5 photogates, 20 cm apart, which were connected to a datalogger for recording when the a lizard crossed a photogate. We ran each lizard twice with an interval of at least 30 min between trials. All locomotor trials were conducted during the lizards' usual activity period (from 9:00 to 19:00). We calculated offspring sprint speed by dividing 20 cm with the fastest time to pass each of the four 20 cm intervals between photogates (Angilletta *et al.*, 2002).

2.4. Statistical analyses We calculated relative litter mass as litter mass divided by female postpartum body mass (Shine, 1980). Body condition of postpartum females was quantified as the residuals of linear regression of log-transformed body mass on log-transformed SVL (Du and Lü, 2009). We used the Shapiro-Wilk test and Fligner-Killeen test to test the normality and homogeneity of all variances. We used the linear mixed-effects model (LME; "nlme" package; Pinheiro *et al.*, 2020) to analyze the effects of treatment and time (fixed factors) on maternal body temperature from the first and second measurements, respectively, with individual identity as a random factor and time as a repeated factor. We also used LME to analyze the effects of measurement sequence and time (as fixed factors) on maternal body temperature in the Control and the Hypoxia treatments, respectively, with individual identity as a random factor and measurement sequence as a repeated factor. One female from the Hypoxia treatment gave birth on the 15th day after acclimation, so we excluded that individual from analyses of the second measurement of maternal body temperature. We used LME to analyze how treatment affected

maternal postpartum body condition and offspring locomotor performance, with experimental container as a random factor. We also used the LME to determine the effects of treatments on litter size, relative litter mass, and offspring size using the initial maternal body mass as the covariate and container as a random factor. We fit a linear mixed-effect model ('lmer' and 'lmerTest: anova' in "lmerTest" package; Kuznetsova *et al.*, 2017) to analyze the effects of treatment (fixed factor) on parturition time with experimental container as a random factor. Differences in substrate (sand) surface temperatures at the cool and hot ends of experimental containers between the two treatments were analyzed with a Kruskal Wallis Test. We conducted all statistical analyses in R (v3.6.1; R Core Development Team, 2019).

3. Results

Thermal regimes (sand surface temperatures) in the Hypoxia treatment were identical to those in the Control treatment (Cool: $\chi^2 = 2.052$, $P = 0.152$; Hot: $\chi^2 = 0.850$, $P = 0.357$). Pregnant females from the Hypoxia treatment had higher body temperatures than did females from the Control treatment during the first measurement session (by 0.51 ± 0.21 °C; $df = 16$, $|t| = 2.411$, $P = 0.028$). However, in the interval between the first and second measurement sessions, pregnant females from the Control treatment raised their body temperatures by 1.25 ± 0.36 °C ($df = 7$, $P = 0.010$), while the body temperatures of females from the Hypoxia treatment did not change significantly ($df = 8$, $P = 0.118$). Overall therefore, we found no significant differences in maternal body temperatures between the two treatment groups during the second measurement session ($df = 15$, $|t| = 0.905$, $P = 0.380$).

In total, 8 (out of 12) females from the Control treatment and 10 (out of 12) females from the Hypoxia treatment gave birth to their offspring successfully. In general, parturition in females from the Hypoxia treatment occurred earlier (21.2 ± 1.0 [mean \pm SE] days since beginning of the acclimation period; 80% of births occurred over days 18–23 of acclimation) than parturition in females from the Control treatment (26.5 ± 1.1 days since acclimation; $F_{1,16} = 12.516$, $P = 0.003$; Figure 1). The Hypoxia treatment had no significant effects on maternal postpartum body condition, or on relative litter mass and litter size (Table 1). Moreover, body mass, snout-vent length, and sprint speed of offspring were unaffected by the hypoxic environment experienced by pregnant females in our experiment (Table 1).

4. Discussion

Our results demonstrated that pregnant females advanced parturition in response to the Hypoxia treatment. However,

Table 1 Maternal postpartum body condition, relative litter mass, and offspring body mass, snout-vent length (SVL), and sprint speed of *Phrynocephalus vlanguaii* in the two treatments.

Traits	Mean \pm SE		Statistical analysis
	Control	Hypoxia	
Litter size	2.0 \pm 0.3	2.7 \pm 0.2	$ d = 1.427, P = 0.290$
Postpartum body condition	0.047 \pm 0.018	0.064 \pm 0.014	$ d = 0.757, P = 0.528$
Relative litter mass (%)	33.2 \pm 3.3	37.1 \pm 2.4	$ d = 0.838, P = 0.490$
Offspring body mass (g)	0.801 \pm 0.043	0.882 \pm 0.022	$ d = 1.340, P = 0.312$
Offspring SVL (mm)	26.34 \pm 0.39	26.15 \pm 0.20	$ d = 0.402, P = 0.727$
Offspring sprint speed (m/s)	0.821 \pm 0.074	0.885 \pm 0.044	$ d = 0.796, P = 0.431$

contrary to our first hypothesis, pregnant females from the Hypoxia treatment did not select lower body temperatures, but instead, thermoregulated to achieve higher body temperatures. More surprisingly, and contrary to our second hypothesis, the hypoxic environment experienced by late-term pregnant females did not impact SVL, body mass or sprint speed of their offspring. Nor did the Hypoxia treatment have any effect on relative litter mass or maternal postpartum body condition.

Previous research has shown that pregnant females select lower body temperatures than do non-pregnant females and males (Beuchat, 1988; Carretero *et al.*, 2005; López-Alcaide *et al.*, 2014). Under hypoxic conditions, non-reproductive individuals have also been found to lower their body temperatures (Tattersall and Gerlach, 2005; Cadena and Tattersall, 2009; Li *et al.*, 2020). In contrast, we found that pregnant females under hypoxic conditions had higher body temperatures than did those from the Control treatment in the first measurement session (Figure 2). This acute behavioral response of late-term pregnant females may be a strategy used to benefit themselves and their offspring in several ways. First, higher body temperatures may optimize the foraging effort (by increasing sprint speed and the ability to catch prey) and digestion efficiency of pregnant females (Ji *et al.*, 1996; Plasman *et al.*, 2019), which may offset the negative impacts of hypoxia on pregnant females and their developing embryos. Second, higher maternal body temperatures might increase the frequency of respiration and lung tidal volume (Davies *et al.*, 1982; Piercy *et al.*, 2015), which may compensate for decreasing oxygen concentration in hypoxic conditions, and sustain the necessary oxygen supply. Third, higher maternal body temperature advances parturition by speeding up the developmental rates of embryos (Deeming and Ferguson, 1991; Griffith *et al.*, 2016), which may reduce the impacts of hypoxia on late-term embryos.

Interestingly, pregnant females from the Control treatment raised their body temperatures during the second measurement session (by 1.25 ± 0.36 °C; $df = 7, P = 0.010$; Figure 2), to achieve body temperatures similar to those of females from the Hypoxia treatment. This finding suggests that viviparous lizards at high altitudes (we mimicked the oxygen condition of an altitude

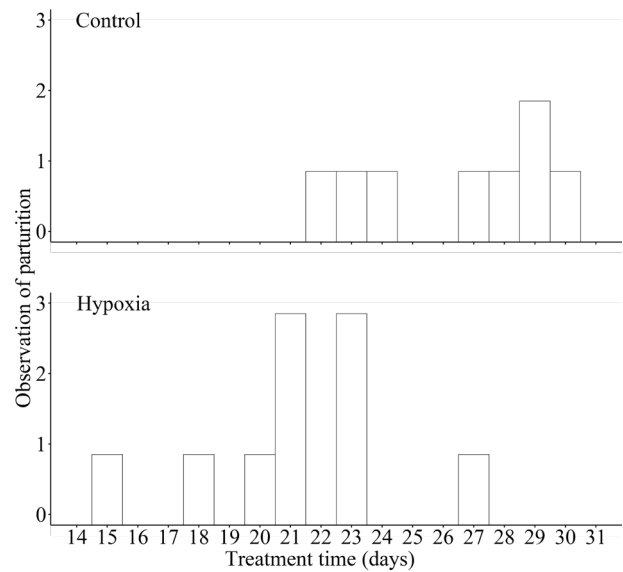


Figure 1 The observation of pregnant females' parturition through time. The histogram indicates the observation counts of females' parturition through time in Control and Hypoxia treatment.

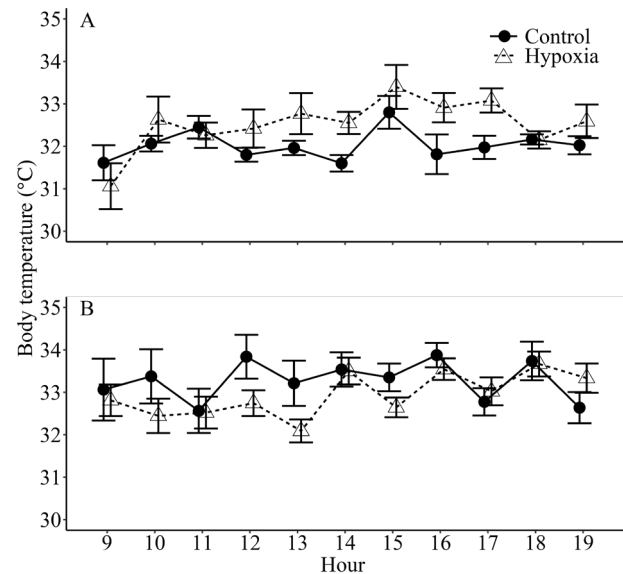


Figure 2 Body temperatures of pregnant females in two treatments and two measurement sessions. Panel A and B represent the first and second measurements, respectively. During each measurement, body temperatures of pregnant females were recorded from 9:00 to 19:00 with 1-hour intervals.

of 3600 m in the Control treatment) may already have been experiencing hypoxic stress during late-term gestation. Our Hypoxia treatment may have exacerbated this stress and forced pregnant females to thermoregulate to higher body temperatures to advance parturition. To further investigate these inferences from our results, future research could analyze inter/intra-specific comparisons between body temperatures and parturition times of pregnant females from species/populations dwelling in habitats with similar temperatures but different oxygen levels.

The advanced parturition we observed in females from the Hypoxia treatment may also be the result of giving birth to premature offspring (although the higher maternal body temperatures should have speeded up embryonic development: Deeming and Ferguson, 1991; Zhang *et al.*, 2010). Producing premature offspring as a response to stress during gestation or incubation has been found in other species (Warkentin, 1995, 2007; Radder *et al.*, 2008). However, the hypoxic environment experienced by late-term pregnant females in our experiment did not affect the SVL, body mass or sprint speed of their offspring (negative effects on these traits are traditionally used to define 'premature' offspring: Cano *et al.*, 2001; Radder *et al.*, 2008). Our results thus suggest that pregnant females exposed to hypoxic conditions during late-term gestation give birth earlier, but to healthy offspring, at least in the short-term. Further studies are needed to investigate if there are any long-term negative effects of hypoxia during development on offspring traits. Pregnant females of an oviparous lizard (*Podarcis muralis*) that were transplanted to a higher altitude with hypoxic conditions also had unaffected postpartum body condition and produced offspring with normal morphology (Kouyoumdjian *et al.*, 2019). Advanced offspring without degraded traits have also been reported in other studies on high-altitude reptiles (Li *et al.*, 2009; Zhang *et al.*, 2010). It is noteworthy that gravid females used in this study were in late-term gestation. Embryos at late developmental stages may be more resistant to hypoxic stress, although they actually have a higher whole-embryo metabolic rate. Future studies could take advantage of seminatural enclosures (where recaptures are possible) to explore long-term effects (e.g. survival, reproduction) of late-gestational hypoxia on offspring fitness.

Our study was designed to explore the impacts of hypoxic environments experienced by upslope-shifting species under a climate warming scenario. The Hypoxia treatment represents an extreme warming scenario that is unlikely to happen in the near future. High-altitude species may still have decades yet, to adapt to the increasingly hypoxic conditions predicted to occur due to global warming, as they move upslope. However, our study demonstrates that, even late-term pregnant females exposed to a hypoxic environment, can produce offspring with normal short-term traits. In conclusion, raising maternal body temperature and advancing parturition are two potentially advantageous responses to the hypoxic stress faced by high-altitude and upslope-shifting species.

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